

Seasonal changes in the stability of male–male bonds in Indian Ocean bottlenose dolphins (*Tursiops* sp.)

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Summary

In Shark Bay, Western Australia, males cooperate in alliances of two or three individuals to herd females. In one closely observed alliance of three males, only two of the three males participated in any given herding event, but there were frequent changes, called 'partner changes', in which two males herded together. The frequency of partner changes was strongly seasonal. In each of two consecutive years the frequency of partner changes was high prior to the breeding season but low during the breeding season. We test the hypothesis that the males had fewer opportunities to change herding partners during the breeding season. This hypothesis was not supported, so we conclude that the high frequency of partner changes prior to the breeding season reflects instability of social bonds. We evaluate these results in reference to hormonal data from a captive study.

Introduction

Male bottlenose dolphins in Shark Bay, Western Australia cooperate in stable alliances of two or three individuals to herd individual females (Connor *et al.*, 1992a,b). During 1987–1989 we documented herding by 10 alliances, including three males that visited the shallows by a camping area where they were provisioned daily with dead fish (Connor & Smolker, 1985, Connor *et al.*, 1992a,b). Before their disappearance in early 1989, we were able to observe herding behaviour by the provisioned males in great detail compared to herding by other males in the bay.

Only two of the three provisioned males herded together at a time; the two males herding together were called 'partners' and the other male the 'odd-male-out'. The alliance of provisioned males often associated with another alliance consisting of two non-provisioned males. Occasionally in 1987, but frequently in 1988, the odd-male-out herded with either member of the other alliance (Connor *et al.*, 1992b). On a given day there was usually one

herding association in the Monkey Mia shallows. This usually involved two of the provisioned males but occasionally the odd-male-out herded with a member of the other alliance. On some days there were two herding associations, involving one female herded by two of the provisioned males and another female herded by the odd male out cooperating with a member of the other alliance.

There were numerous changes in which two of the three provisioned males were partners. The frequency of these partner changes was strongly seasonal (Connor *et al.*, 1992b). Here we evaluate competing hypotheses to explain the seasonal shift in frequency of partner changes.

Results

In 1987 and 1988 more partner changes occurred per month during the austral winter (May–August) than during the austral spring–summer (September–December) (Mann–Whitney *U*-test, $U=0$, $P=0.001$). In both years, the number of partner changes peaked in July–August before an abrupt reduction beginning in September (Fig. 1). September marks the beginning of the mating season in Shark Bay, as defined by the time of births (given a 12 month gestation period; Connor *et al.*, in press, Richards *et al.*, in prep.).

What might account for this dramatic August–September shift in the stability of herding partners among the three provisioned males? Paralleling the drop in frequency of partner changes was a September–December increase in the proportion of days each month in which at least one of the provisioned males herded a female (Mann–Whitney *U*-test, $U=6$, $P=0.011$). This increase in herding was not due to an increase in the number of herding events per month in summer versus winter (Mann–Whitney *U*-test, $U=35$, $P=0.44$), but to longer herding events in the summer months. A larger proportion of herding events lasted four or more days during the summer period ($G=8.974$, $P=0.003$).

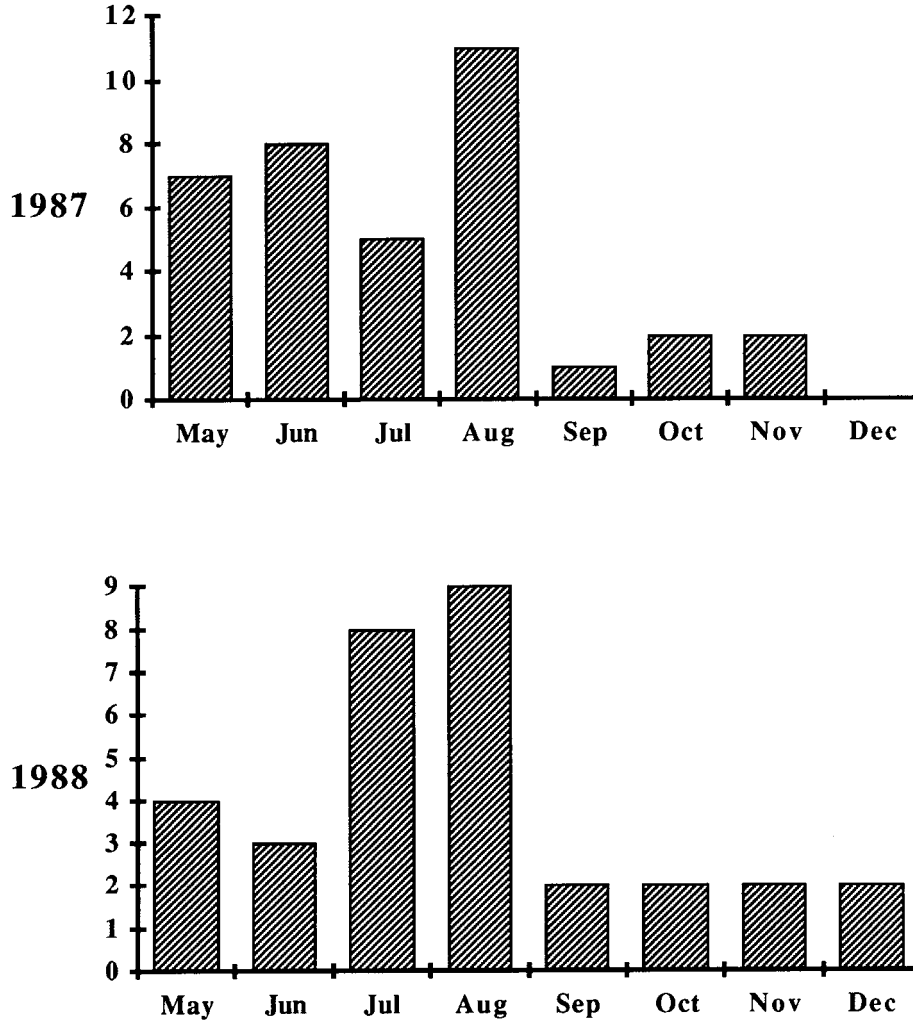


Figure 1. Seasonal changes in partner change frequency for 1987 and 1988. The bars represent the number of partner changes that occurred in each month. Data are not available for December 1987. More partner changes occurred in the winter months (May–August) than in the spring and summer months (September–December) (Mann–Whitney U -test, $P=0.001$). From Connor *et al.*, 1992b.

One hypothesis for the seasonal shift in partner stability is that there were fewer opportunities for partner changes during the summer. Nearly all partner changes occurred between herding events. Therefore, if the males herded for longer periods in the summer, there may have been fewer opportunities to switch partners. This 'reduced opportunity' hypothesis predicts no difference in the proportion of opportunities in which partner changes occurred between winter and summer.

Alternatively, the observed shifts in the frequency of partner changes may reflect changes in the stability of social bonds. If partner changes occurred during a smaller proportion of opportunities in the

summer months, this 'social instability' hypothesis is supported.

We tested the 'reduced opportunity' hypothesis by comparing the proportion of opportunities for partner changes in which a partner change occurred in the period May–August versus September–December. Although, conceivably, a partner change can occur at any time, nearly all occurred between herding associations (we only observed one partner change occur during a herding association). We thus define an opportunity as any interval in which none of the three provisioned males was herding a female. Our definition of 'opportunity' excludes five partner changes from the period

May–August in Fig. 1 because these five partner changes defined the herding events (see Connor *et al.*, 1992b). It is possible (but unlikely) that the five partner changes occurred while the female was being herded, thus they are excluded. Excluding these cases biases the test in favor of the reduced opportunity hypothesis. The two partner changes from November 1987 (Fig. 1) were eliminated because they involved a provisioned male shifting partners from a provisioned male to a member of the non-provisioned alliance while the odd-male-out was herding with the other non-provisioned male. The alternative to excluding these partner changes is to expand the definition of ‘opportunity’ to include opportunities to switch to a non-provisioned male when the odd-male-out is herding. This would greatly expand the number of opportunities during September–November 1987 and thus favor the ‘social competition’ hypothesis since such a partner change only occurred once.

The reduced opportunity hypothesis is not supported: partner changes occurred in 50 of 93 opportunities in the winter months but only 11 of 49 opportunities during the summer months for 1987–88 combined ($G=13.441$, $P<0.001$). We conclude that the seasonal shift in the frequency of partner changes among the males owes to changes in the stability of social bonds.

Discussion

The seasonal change in stability of male bonds among the three provisioned males in Shark Bay may have a hormonal correlate. A 28 month study of a single male *Tursiops* in Hawaii revealed a marked surge in plasma testosterone levels several weeks prior to each of three consecutive breeding seasons (Schroeder & Keller, 1989). Testosterone levels then declined to low levels during the breeding season (<10 ng/ml), when sperm production and concentration were highest (Schroeder & Keller, 1989). The testosterone surge in this captive male occurred at the same time relative to the breeding season as the period of greatest instability in male-male bonds in Shark Bay. In other seasonally breeding mammals, rising testosterone levels prior to the breeding season may trigger behavioral and morphological changes that prepare a male for competition with other males. For example, under the influence of increasing testosterone levels prior to the rut, red deer stags (*Cervus elaphus*) begin antler cleaning, and experience growth of the mane, testes, and neck muscles (Lincoln, 1971). Similarly, the July–August instability of male-bonds in Shark Bay might reflect male attempts to prepare for the breeding season by improving their social position. Competition within an alliance may be high prior to the breeding season as males compete for or ‘test’

herding partners. Alternatively, instability prior to the mating season may reflect lower levels of competition; i.e., males may more readily give up their position as a partner before the mating season when there are fewer opportunities to inseminate females. We cannot presently distinguish among these two hypotheses.

The male in the Hawaiian captive study was exposed to 4–6 reproductively mature females who were kept in adjacent seawater pens separated by wire mesh. The low levels of testosterone (<10 ng/ml) during the breeding season is surprising given the level of male-male aggression during the breeding season in Shark Bay. Wells *et al.* (1987) reported that testosterone levels in adult free-ranging males in Sarasota Bay, Florida were typically greater than 10 ng/ml during the breeding season. Together, these observations suggest that male testosterone levels during the breeding season might depend on factors such as the presence of rival males (e.g. see Wingfield *et al.*, 1990). This issue could be resolved by measuring plasma levels of free-testosterone in adult males in experimentally manipulated social groups.

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